UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 18, No. 1, pp. 1-10

September 24, 1968

The Genera of Phyllomedusine Frogs (Anura: Hylidae)

BY

WILLIAM E. DUELLMAN

UNIVERSITY OF KANSAS
LAWRENCE
1968

University of Kansas Publications, Museum of Natural History

Editors of this number: Frank B. Cross,
Philip S. Humphrey, J. Knox Jones, Jr.

Volume 18, No. 1, pp. 1-10
Published September 24, 1968

University of Kansas
Lawrence, Kansas

PRINTED BY
ROBERT R. (BOB) SANDERS, STATE PRINTER
TOPEKA, KANSAS
1968

32-3687

The Genera of Phyllomedusine Frogs (Anura: Hylidae)

BY

WILLIAM E. DUELLMAN

One of the most distinctive phyletic lines among the diverse Neotropical hylid frogs is composed of a group of 40 species placed in the genus *Phyllomedusa* (Funkhouser, 1957) or in two or three different genera (Goin, 1961; Lutz, 1966). These species differ from all other Neotropical hylids by possessing a vertical, instead of horizontal, pupil. The only other hylids having a vertical pupil belong to the Papuan genus *Nyctimystes*. Goin (1961) erroneously stated that *Nyctimantis* and *Triprion* have vertical pupils.

Although limited information is available on the cytotaxonomy of hylids, the data show that phyllomedusine species have $n = 13$ ($2n = 26$) chromosomes. *Acris* has $n = 11$ ($2n = 22$) (Cole, 1966). Members of the *Hyla leucophyllata, microcephala,* and *parviceps* groups have $n = 15$ ($2n = 30$), *Gastrotheca ceratophrys* has a haploid number of 14, the Papuan hylid genus *Nyctimystes* and all but one of the Australo-Papuan *Hyla* for which the numbers are known have a haploid number of 13, and all other New World hylids studied have $n = 12$ ($2n = 24$) (Duellman and Cole, 1965; Duellman, 1967).

Cei (1963) and Cei and Erspamer (1966) noted that phyllomedusine frogs differ notably from other Neotropical hylids on the basis of the amines and polypeptides in the skin. All species of phyllomedusines deposit their eggs in a gelatinous mass on leaves or branches above water. Although this type of egg deposition is characteristic of some rhacophorines and apparently all centrolenids, it is known among hylids only in the phyllomedusines and in two species of *Hyla*.

The distinctive combination of morphological, physiological, chromosomal, and behavioral characteristics is strongly suggestive that these frogs represent an early phyletic divergence within the Hylidae. Günther (1859) proposed the familial name Phyllomedusidae for *Phyllomedusa bicolor* (Boddaert). I suggest the recognition of the group as a subfamily. The following classification of

the phyllomedusines is based on my own knowledge of the Middle American and some South American species and on evidence from the literature on those South American species with which I am not personally familiar.

Subfamily Phyllomedusinae Günther, 1859

Phyllomedusidae Günther 1859 [Type genus, *Phyllomedusa* Wagler, 1830].

Definition.—Moderately small to large hylids having vertical pupils, $n = 13$ $(2n = 26)$ chromosomes, skin containing large amounts of powerful bradykinin-like and physalaemin-like polypeptides, eggs suspended from vegetation above water, and tadpoles have a ventral spiracle sinistral to midline.

Range.—Low and moderate elevations in South and Middle America, including Trinidad, from northern Argentina and northwestern Ecuador to Veracruz and southern Sonora, México.

Content.—Three genera, one of which probably is composite.

Genus Agalychnis Cope, 1864.

Agalychnis Cope, 1864 [Type species, *Hyla moreletii* Duméril, 1853, by subsequent designation].

Definition.—Fingers and toes at least half webbed; terminal discs large; first toe shorter than second and not opposable to others; skin smooth, lacking osteoderms; parotoid glands, if present, poorly developed and diffuse; palpebral membrane reticulate (except in *A. calcarifer*); iris red or yellow; skull shallow, depth less than 40 per cent of length; nasals large; frontoparietal fontanelle large; quadratojugals reduced; prevomerine teeth present.

Range.—Central Veracruz and northern Oaxaca, México, southeastward through Central America to northwestern Ecuador; one species disjunct in Amazonian Ecuador.

Content.—Eight species [synonyms in brackets]: *annae* (Duellman, 1963); *calcarifer* Boulenger, 1902; *callidryas* (Cope, 1862) [*helenae* Cope, 1885; *callidryas taylori* (Funkhouser, 1957)]; *craspedopus* (Funkhouser, 1957); *litodryas* (Duellman and Trueb, 1967); *moreleti* (Duméril, 1853) [*holochroa* (Salvin, 1861)]; *saltator* Taylor, 1955; *spurrelli* Boulenger, 1913.

Remarks.—Savage and Heyer (1967) provided evidence that *A. callidryas taylori* (Funkhouser) and *A. helenae* Cope were junior synonyms of *A. callidryas* (Cope).

Genus Pachymedusa, new genus

Type species, *Agalychnis dacnicolor* Cope, 1864.

Definition.—Fingers and toes having basal webs and lateral fringes; terminal discs large; first toe shorter than second and not opposable to others; skin smooth or shagreened, lacking osteoderms; paratoid glands present, diffuse; palpebral membrane reticulate; iris golden yellow with black reticulations; skull deep, depth more than 50 per cent of length; nasals large; frontoparietal fontanelle moderately large; quadratojugal robust; prevomerine teeth present.

Range.—Pacific slopes and lowlands from southern Sonora to the Isthmus of Tehuantepec, México.

Content.—Monotypic: *dacnicolor* Cope, 1864 [*alcorni* Taylor, 1952].

Remarks.—The generic name is derived from the Greek *pachy* meaning thick and the Greek *Medousa* (Latin, *Medusa*) in reference to *Phyllomedusa*; the sense implied is the heavy body of *Pachymedusa dacnicolor*.

Genus Phyllomedusa Wagler, 1830

Phyllomedusa Wagler, 1830 [Type species, *Rana bicolor* Boddaert, 1772].

Pithecopus Cope, 1866 [Type species, *Phyllomedusa azurea* Cope, 1862 (= *Phyllomedusa hypochondrialis* Daudin, 1803), by original designation].

Hylomantis Peters, 1872 [Type species *Hylomantis aspera* Peters, 1872, by monotypy].

Phrynomedusa Miranda-Ribeiro, 1923 [Type species, *Phrynomedusa fimbriata* Miranda-Ribeiro, 1923, by subsequent designation].

Bradymedusa Miranda-Ribeiro, 1926 [Type species, *Bradymedusa moschada* Miranda-Ribeiro, 1926 (= *Phyllomedusa rohdei* Mertens, 1926) by subsequent designation].

Definition.—Fingers and toes having greatly reduced webbing or lacking webs; terminal discs small; first toe shorter than, equal to, or longer than second, opposable or not; skin smooth or rugose having osteoderms or not; parotoid glands present, in most species, usually distinct and elevated; palpebral membrane not reticulate; iris uniformly silvery white to orange-bronze with black reticulations; skull moderate to deep, depth more than 38 per cent of length; nasals moderately small; frontoparietal fontanelle present, variable in size; quadratojugal reduced in some species; prevomerine teeth present or absent.

Range.—Low and moderate elevations in South America east of the Andes from the Caribbean (including Trinidad) to northern Argentina; Costa Rica and Panamá in Central America.

Content.—Thirty-one species [synonyms in brackets]: *aspera* (Peters, 1872); *ayeaye* (B. Lutz, 1966); *bahiana* A. Lutz, 1925; *bicolor* (Boddaert, 1772) [*scleroderma* Cope, 1868]; *blombergi* Funkhouser, 1957; *boliviana* Boulenger, 1902; *buckleyi* Boulenger, 1882; *burmeisteri burmeisteri* Boulenger, 1882; *burmeisteri distincta* B. Lutz, 1950; *centralis* Bokermann, 1965; *cochranae* Bokermann, 1966; *coelestis* (Cope, 1874); *edentula* Andersson, 1945; *feltoni* Shreve, 1935; *fimbriata* (Miranda-Ribeiro, 1923) [*appendiculata* A. Lutz, 1925]; *guttata* A. Lutz, 1925; *hypochondrialis* (Daudin, 1803) [*azurea* Cope, 1862; *megacephala* (Miranda-Ribeiro, 1926)]; *iheringi* Boulenger, 1885; *lemur* Boulenger, 1882; *loris* Boulenger, 1912; *medinae* Funkhouser, 1962; *nicefori* Barbour, 1926; *orcesi* Funkhouser, 1957; *pailona* Shreve, 1959; *perlata* Boulenger, 1882; *rohdei* Mertens, 1926 [*moschada* (Miranda-Ribeiro, 1926)]; *sauvagei* Boulenger, 1882 [*rickettsii* Günther, 1897]; *tarsius* (Cope, 1868); *tomopterna* (Cope, 1868) [*palliata* Peters, 1872]; *trinitatis* Mertens, 1926, *vaillanti* Boulenger, 1882, *venusta* Duellmann and Trueb, 1967.

Remarks.—Phyllomedusa includes 1) a series of large species (*bicolor-burmeisteri*) showing progressive specialization of the feet; 2) a series of small species having grasping feet (*ayeaye, centralis, cochranae, guttata, hypochondrialis,* and *rohdei*); 3) a series of small, relatively unspecialized species (*lemur, loris,* and *medinae*); and 4) several other species of questionable affinities. Lutz (1966) resurrected Cope's (1866) *Pithecopus* for 12 species (*ayeaye, boliviana, burmeisteri, coelestis, hypochondrialis, nicefori, rohdei, sauvagei, tarsius, tomopterna, trinitatis,* and *vaillanti*). Adequate material is not available for detailed study of all South American species; consequently, a firm classification cannot be established at this time. Nevertheless, it is obvious that Lutz's arrangement is unnatural. If subsequent investigations show, as seems likely, that the small specialized phyllomedusines are a natural phyletic unit, the generic name *Pithecopus* is available. However, species such as *boliviana, burmeisteri, nicefori,* and *trinitatis* do not belong in *Pithecopus.* As noted by Funkhouser (1962), the small, relatively unspecialized species (*lemur, loris,* and *medinae*) form a natural group; possibly this group should be accorded generic recognition. Until more evidence on the interspecific relationships is acquired, the maintenance of the current classification is desirable.

DISCUSSION

Noble (1931) considered the species of *Phyllomedusa* having opposable digits, reduced terminal discs, and no webbing to be advanced and such species as *Agalychnis moreleti, calcarifer,* and *spurrelli* to be primitive. Funkhouser (1957) followed Noble's suggestion and attempted to explain the evolution of the species of *Phyllomedusa* (*sensu lato*) by assuming that they evolved from an advanced *Hyla*-like ancestor. Therefore, she placed those species having large, fully webbed hands and feet near the base of her phylogenetic scheme and hypothesized that evolutionary sequences involved stages of reduction and eventual loss of webbing, followed by the development of grasping toes. Such an evolutionary history is highly unlikely. The *Agalychnis* phyletic line has one kind of specialization for an arboreal existence. It is contrary to evolutionary theory that a specialized group would evolve into a generalized form and then evolve new kinds of specializations to meet the needs imposed by the same environmental conditions affecting the earlier specialized group. A more reasonable hypothesis is that the evolution of opposable digits took place in a phyletic line that had as its ancestral stock a frog with generalized hands and feet. If this assumption is correct, *Phyllomedusa* and *Agalychnis* represent different phyletic lines; each exhibits divergent modes of adaptation for arboreal habits, whereas *Pachymedusa* probably remains relatively little changed from the basic phyllomedusine stock.

On the basis of modern distribution and areas of diversification alone (no fossils are known), it is evident that *Phyllomedusa* underwent its adaptive radiation in South America, *Agalychnis* evolved in Central America, and *Pachymedusa* ended up in western México. If we follow the Matthewsian concepts of the American herpetofauna outlined by Dunn (1931) and modified by Schmidt (1943) and Stuart (1950), *Pachymedusa* represents a "hanging-relict" of a group that moved southward. According to Savage's (1966) interpretation of the origins and history of the American herpetofauna, *Agalychnis* and *Pachymedusa* are members of the Mesoamerican fauna, and *Phyllomedusa* is part of the Neotropical fauna. Perhaps the phyllomedusines arose in South America; from there a primitive stock spread northward and survived as *Pachymedusa* in México, whereas the stock in Central America and South America evolved into *Agalychnis* and *Phyllomedusa,* respectively.

Evidently the primitive phyllomedusines evolved the habit of arboreal egg deposition and a walking gait; the latter is best developed in the small, highly specialized species of *Phyllomedusa* (Lutz, 1966). Probably the other divergent arboreal adaptations resulted from environmental stresses and competition. The generalized *Pachymedusa* inhabits relatively dry areas characterized by low forest. Throughout its range it coexists with no more than five other arboreal hylids. The species of *Agalychnis* live in rain forests and humid montane forests. In any given area one species of *Agalychnis* occurs sympatrically with no more than a dozen other arboreal hylids. With few exceptions the species of *Agalychnis* are more arboreal in their habits than are other hylids. The species of *Phyllomedusa* live in the same kinds of habitats as do those of *Agalychnis,* but throughout the ranges of most of the species of *Phyllomedusa* the diversity of arboreal hylids is much greater than in Central America. In the upper Amazon Basin as many as 35 hylids occur sympatrically. Many groups of *Hyla* in this area (for example, the *Hyla boans* and *Hyla marmorata* groups) are equally as arboreal in their habits as are the species of *Agalychnis* in Central America. Conceivably, competition within this array of tree frogs resulted in selection for modification of the extremities, thereby bringing about a different mode of climbing in *Phyllomedusa.* The walking gait already present in phyllomedusines provided a source for further modification, which resulted in the development of opposable digits and the associated lemuroid manner of climbing.

The known life histories of most species of *Phyllomedusa,* all species of *Agalychnis,* and that of *Pachymedusa* are similar. Characteristically the tadpoles are generalized pelagic types that develop in ponds, but at least some of the small specialized *Phyllomedusa* in southeastern Brazil have stream-adapted tadpoles with funnel-shaped mouths (Cochran, 1955; Bokermann, 1966). Knowledge of the life histories of the other species of *Phyllomedusa* should aid in the interpretation of the phylogenetic relationships of the several groups of frogs now assigned to that genus.

ACKNOWLEDGMENTS

I am grateful to Linda Trueb who provided the osteological data included, and who helped me in formulating some of the ideas expressed in the discussion. This paper is a result of investigations on hylid frogs supported by the National Science Foundation (NSF-GB-5818).

LITERATURE CITED

BOKERMANN, W. C. A.
1966. A new *Phyllomedusa* from southeastern Brazil. Herpetologica, 22:293-297.

CEI, J. M.
1963. Some precipitin tests and preliminary remarks on the systematic relationships of four South American families of frogs. Bull. Serological Mus., 30:4-6.

CEI, J. M. and V. ERSPAMER
1966. Biochemical taxonomy of South American amphibians by means of skin amines and polypeptides. Copeia, no. 1:74-8.

COCHRAN, D. M.
1955. Frogs of southeastern Brazil. Bull. U. S. Natl. Mus., 206; xvi + 423 pp.

COLE, C. J.
1966. The chromosomes of *Acris crepitans blanchardi* Harper (Anura: Hylidae). Copeia, no. 3:578-580.

COPE, E. D.
1864. Contributions to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 16:166-181.
1866. On the structures and distribution of the genera of arciferous Anura. Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 6:67-112.

DUELLMAN, W. E.
1967. Additional studies on chromosomes of anuran amphibians. Syst. Zool., 16:38-43.

DUELLMAN, W. E. and C. J. COLE
1965. Studies of chromosomes of some anuran amphibians (Hylidae and Centrolenidae). Syst. Zool., 14:139-143.

DUMÉRIL, A. H.
1853. Memoire sur les batraciens anoures de la famille des hylaeformes ou rainettes comprenant la description d'un genre nouveau et de onze especès nouvelles. Ann. Sci. Nat., ser. 3, 19:135-179.

DUNN, E. R.
1931. The herpetological fauna of the Americas. Copeia, no. 3:106-119.

FUNKHOUSER, A.
1957. A review of the Neotropical tree-frogs of the genus *Phyllomedusa*. Occas. Papers Nat. Hist. Mus., Stanford Univ., 5:1-90.
1962. A new *Phyllomedusa* from Venezuela. Copeia, no. 3:588-590.

GOIN, C. J.
1961. Synopsis of the genera of hylid frogs. Ann. Carnegie Mus., 36:5-18.

GÜNTHER, A. C. L. G.
"1858" [1859]. Catalogue of the Batrachia Salientia in the collection of the British Museum. Taylor and Francis, London, xvi + 160 pp., 12 pls.

LUTZ, B.
1966. *Pithecopus ayeaye*, a new Brazilian hylid with vertical pupils and grasping feet. Copeia, no. 2:236-240.

MIRANDA-RIBEIRO, A. DE
1923. As Phyllomedusas do Museu Paulista. Bol. Mus. Nac., Rio de Janeiro, 1:3-6.
1926. Notas para servirem ao estudo dos gymnobatrachios (Anura) brasileiros. Arch Mus. Nac., Rio de Janeiro, 27:1-227, pls. 1-22.

NOBLE, G. K.
1931. The biology of the Amphibia. McGraw-Hill, New York, 577 pp.

PETERS, W. C. H.
1872. Über eine, zwei neue Gattungen enthaltende, Sammlung von Batrachiern des Hrn. Dr. O. Wucherer aus Bahia, so wie übereinige neue oder weniger bekannte Saurier. Monatsb. Akad. Wiss. Berlin, 1872: 768-776.

SAVAGE, J. M.
1966. The origins and history of the Central American herpetofauna. Copeia, no. 4:719-766.

SAVAGE, J. M. and W. R. HEYER
1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna, 5:111-131.

SCHMIDT, K. P.
1943. Corollary and commentary for "Climate and Evolution." Amer. Midl. Nat., 30:241-253.

STUART, L. C.
1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Contr. Lab. Vert. Biol., Univ. Michigan, 45:1-77, pls. 1-9.

WAGLER, J. G.
1830. Näturliches System der Amphibien, mit vorangehender Classification der Saügethiere und Vögel. München, vi + 354 pp., 9 pls.

Transmitted April 18, 1968.

□